

LUNAR AND TIDAL PERIODICITY OF MOLTING AND
REPRODUCTION IN STOMATOPOD CRUSTACEA:
A SELFISH HERD HYPOTHESIS

MARJORIE LINDQUIST REAKA

Department of Zoology, The University of Maryland, College Park, Maryland 20742

One of the constraints imposed upon arthropods by their protective exoskeleton is the necessity to molt. While the physiology and morphogenesis associated with the molt cycle in crustaceans has commanded a great deal of attention (*e.g.*, Passano, 1960; Drach and Tchernigovtzeff, 1967; Stevenson, 1972; Aiken, 1973; Davis, Fyhn, and Fyhn, 1973; Reaka, 1975a), few workers have examined the process of molting in an evolutionary perspective. This study examines the ecological and evolutionary consequences of molting in stomatopod crustaceans.

Mantis shrimp are primitive members of the Malacostraca (Brooks, 1962; Siewing, 1963; Holthuis and Manning, 1969; Schram, 1969a, b, 1973; Burnett and Hessler, 1973; Reaka, 1975b), but they possess a highly specialized life style which may be associated with unique molting and reproductive adaptations. Stomatopods frequently live in species assemblages where as many as five congenics occupy indistinguishable microhabitats in one tidepool (Reaka, 1972, and in preparation) and seven congenics may occupy one tide flat (this study). Protection from predation is afforded by burrows or cavities in mud, sand, rocks or coral. Stomatopods employ intense and sometimes lethal agonistic behavior against conspecifics and congenics while fighting to obtain or retain burrows and in addition are rapacious carnivores.

All crustaceans are susceptible to conspecific or other predators when molting and often possess behavioral adaptations to minimize mortality at this time (Passano, 1960). This vulnerability is considerably magnified in molting stomatopods because of their behavior and frequent sympatry with closely related species; if not killed by another mantis shrimp, a stomatopod may be displaced from its hole and exposed to predation by fishes (Townesley, 1953; Camp, 1973). Large size is an obvious advantage for pursuit and overpowering of prey, defense against predators, conspecific and congeneric fighting, and reproduction (Reaka, 1974, 1975c), but carries the disadvantage of repeated molts. How, then, do stomatopods minimize the effects of molting while maintaining their tactics of predation and contest competition? Reclusive and submissive behavior, as well as sealing the entrance of the burrow, reduce vulnerability at the molt in stomatopods; the stages of morphogenesis associated with incapacitation and exuviation are abbreviated in several aggressive taxa of crustaceans but especially in stomatopods; and asymmetrical stages of the molt cycle suggest that the early premolt may be a waiting period, whereupon initiation of the molt progresses rapidly following the correct cue (Reaka, 1975a). The present paper examines timing of molting and reproduction, and suggests that lunar and tidal synchrony of molting in the population

may reduce mortality due to conspecific and congeneric aggression according to a temporal model of the selfish herd hypothesis (Hamilton, 1971).

MATERIALS AND METHODS

Data on field and laboratory molting and reproduction were collected over several years in populations of *Gonodactylus zacae* (La Paz Bay, Gulf of California, Mexico). *G. zacae* was returned immediately to Berkeley where individuals were isolated in plastic aquaria at room temperature (19–26° C) with normal laboratory illumination. Group 1 (N = 36) was maintained from June 1971 until February 1972; group 2 (N = 31) from November 1971 until July 1972; group 3 (N = 51) from March 1972 until September 1972; group 4 (N = 83) from October 1972 to July 1973; group 5 (N = 27) from May 1973 to September 1973.

G. fulcatus from Kaneohe Bay, Hawaii, was maintained in the laboratory at the Hawaii Institute of Marine Biology (HIMB) in similar conditions (about 26° C, laboratory illumination). In addition, some individuals occupied perforated containers in circulating seawater tables (about 26° C, natural photoperiod). *G. fulcatus* was maintained in Hawaii during August, September, and early October (1971), September (1972), and October (1973), before shipment to Berkeley where maintenance was as described for *G. zacae* (group 1, N = 149, was maintained until August 1972; group 2, N = 59, until April 1973; group 3, N = 54, until March 1974).

Haptosquilla glyptocercus from Eniwetok Atoll, Marshall Islands, was maintained in closed containers at the Eniwetok Marine Biological Laboratory (about 27° C, natural photoperiod) during August and September 1972 before being shipped to Berkeley and maintained as described above until April 1973.

Pseudosquilla ciliata from Kaneohe Bay, Hawaii, was maintained at HIMB during September and early October 1971, and at Berkeley until March 1972 (N = 11); and also at Berkeley from February until June 1974 (N = 38). The conditions in which *P. ciliata*, shipped from Panama, Florida, was maintained in Berkeley (February to June 1974, N = 32) were the same as described above.

Field and laboratory data from one Australian gonodactylid community include five species which were collected from Cockle Bay and Geoffrey Bay on Magnetic Island near Townsville, Queensland, from August until October 1973. In Australia these species were maintained in the laboratory (about 23° C, natural photoperiod and sometimes artificial lighting) in either plastic aquaria, or briefly in perforated plastic bottles floated in circulating sea water aquaria. After shipment to Berkeley, they were maintained as described above until April 1974.

Data on molting and reproduction from a similar community of gonodactylids in Thailand includes seven species from one reef flat. These species were collected and maintained in the laboratory at the Phuket Marine Biological Center from July until August 1973, and from June until August 1974, using the same procedures described above (normal laboratory illumination and laboratory water temperatures approximating 26° C).

The size range among the ten species of gonodactylids presented in this study varies from juveniles (10 mm total length) to adults (90–100 mm total length in the largest species). Molting rates do not vary over ontogeny within species of stomatopods; therefore the size distribution of individuals maintained did not

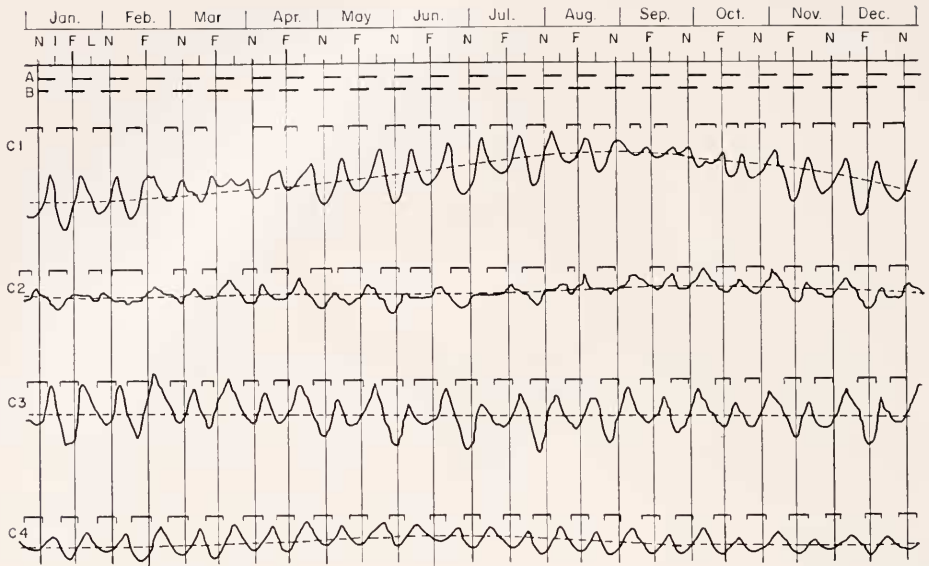


FIGURE 1. Lunar and tidal cycles at various sites for 1973, showing time divisions of the initial lunar (A), the divided lunar (B), and actual tidal (C) methods of analysis. C1 represents tidal curve at Guaymas, Mexico; C2, Honolulu, Hawaii; C3, Townsville, Australia; and C4, Phuket, Thailand. Dashed lines represent mean tidal levels used to define spring and neap tides. Differences in extremity of tidal curves are due to differences in the base tidal datum used in different countries.

affect incidence of molting. All animals were maintained individually in containers of appropriate size and volume ($10 \times 10 \times 10$ cm and $10 \times 10 \times 20$ cm plastic boxes, and plastic bowls and aquaria of various sizes). All containers were provided with sand or gravel substrate and an Erlenmeyer flask painted black or pieces of coral for habitation. Individuals were fed pieces of fish, crustaceans, and mollusks twice or thrice weekly, and the sea water was changed later the same day. In all cases maintenance temperatures approximated field conditions. Although temperature and photoperiod were not rigorously controlled, they should have produced no systematic bias across lunar or tidal phases. Individuals were checked for molts and eggs daily or at most every two days.

When dealing with a temporally variable phenomenon, the problem arises of how to construct categories which encompass most of the events clustered in time rather than categories which bisect and therefore disguise the frequency modalities. This study used three methods of analysis which divided the lunar and tidal month into equal, logically derived units, and which were devised before beginning data analysis. Therefore, use of one or the other method does not represent any transformation or exaggeration of categories but indicates different ways of dividing a month into four equal divisions in order to encompass existing modalities. Figure 1 demonstrates the "initial lunar method," the "divided lunar method," and the "actual tidal method" of analysis. For the initial lunar analysis, a lunar calendar was used to identify the apex of the new (N), first (I), full (F), and last (L)

quarter of each lunar month. This day was defined as the initial day of that lunar phase, and all molts or eggs were recorded which fell on that day and in the subsequent six to seven days before the apex of the next phase. This method therefore included events which occurred during the transitional stages between lunar phases, which may serve as cues for organisms. The divided lunar method attempted to encompass events which occurred during a complete lunar phase; for example, molts which occurred in the three days prior to the apex of the full moon, on the day of the full moon, and during the four days subsequent to the full moon were included in the F category. NF and IL indicate that data are derived from N + F and I + L categories. For the actual tidal method of analysis, the lowest tide of each day was recorded from tide tables. A mean tidal curve for the year was drawn through the bimonthly tidal cycles thus derived (dashed line, Fig. 1). All days in which the daily low tide fell below this mean curve were defined as spring tides, and all days in which the daily low was greater than the mean curve were defined as neap tides. The mean tidal curve provided that approximately equal numbers of days were represented in the spring and neap tidal categories over the year, and incorporated seasonal variation in tidal heights in some areas, particularly the Gulf of California.

In the tables and text, an asterisk indicates $P < 0.05$ and a double asterisk indicates $P < 0.01$ that the null hypothesis is correct. All χ^2 tests were repeated using Yates correction for continuity (Siegel, 1956, p. 109). However, in no case did this calculation alter the level of statistical significance; also, Lewontin and Felsenstein (1965) indicate that this correction need not be used. Therefore, only the original χ^2 values are presented.

RESULTS

Repeated observations from field collecting and laboratory maintenance suggested a clustering in time of molts and batches of eggs laid. Table I summarizes molts and eggs laid during lunar and tidal phases over several years using the initial lunar method of analysis. It was impractical to construct and analyze exact tidal curves from all sites over several years. Therefore, in this table the tidal categories are the sum of the molts and eggs occurring during the two associated lunar phases. In the Gulf of California and Hawaii, NF phases (new and full, initial lunar method) correspond in general to neap tides or to the transition from spring to neap tidal cycles ("neap"), while IL (first and last) phases correlate with spring tides or to the transition from neap to spring tidal cycles ("spring"; see Fig. 1).

Gonodactylus zaca (Gulf of California)

In female *G. zaca* there is a strong bimodal trend in numbers of molts over the lunar cycle; most molts occur during "neap" tides (Table I). Males seem to show a monthly lunar rather than a tidal cycle, with reduced molting during the first quarter and increased molting around the last quarter ($L > I$, $\chi^2 = 5.00^*$, $df = 1$). However, this may be an artifact of small sample size, since the frequency distributions of molting males and females may not be significantly different ($P < 0.10$) across lunar phases ($\chi^2 = 6.84$, $df = 3$) and tidal cycles ($\chi^2 = 3.75$,

df = 1). Fewer molting males than females results from fewer males than females in the population rather than lower molting rates of males.

Although oviposition in *G. sacae* appears to occur more commonly during "neap" tides, these data fall below the 0.05 confidence level. However, the distribution of oviposition across tidal categories does not differ from that of molting in *G. sacae*, either in females ($\chi^2 = 0.23$, df = 1) or in the total population ($\chi^2 = 0.00$, df = 1). Also, the distribution of oviposition across "spring" and "neap" tidal phases in *G. sacae* is not significantly different from oviposition patterns in *G. falcatus* ($\chi^2 = 0.35$, df = 1).

Each of the five groups of *G. sacae* was collected during a single lunar phase or a transitional phase. In group 1 (collected during L) a total of 13, 5, 11, 8 molts occurred in the four respective lunar phases; for groups 2 and 4 (collected during I), a total of 27, 10, 24, 11 molts occurred in the four lunar phases; and 4, 1, 7, 8 and 3, 3, 5, 2 molts occurred in groups 3 and 5 which were collected during the I-F transition and during N, respectively. Therefore, time of collection does not appear to set the molting rhythm. There is no apparent change in the pattern of molting in lunar periods with increased time spent in laboratory conditions. Molting rates do not decline with increased maintenance time; and there is no demonstrable effect of time of year or reproductive season upon number of molts or intermolt interval (Reaka, 1975c, and in preparation).

Stomatopods do not cement eggs to appendages and have no obligatory molt before oviposition. In three cases in which female *G. sacae* laid eggs between molts in the laboratory, oviposition occurred 41%, 51%, and 59% through the intermolt intervals of several months; and one *G. sacae* was found in the field with eggs at the eyespot stage (probably one to two weeks old) and with an exuvium in her cavity. Therefore, it seems unlikely that there is a relationship between oviposition and a stage of the molt cycle which might explain the molting synchrony of females. Eggs from *G. sacae* were found in the field or in the laboratory only from March 31 through November, although animals were maintained year round. There is no significant difference ($\chi^2 = 3.59$, df = 3) between lunar molting synchrony of females during the eight months of this reproductive season (22, 9, 27, 12, respectively) and the nonreproductive period (15, 5, 7, 4, respectively).

In summary, the bimodal molting synchrony of female *G. sacae* does not appear to be due to collecting artifact, laboratory conditions, reproductive patterns or seasons. Males of *G. sacae* either show a monthly molting pattern or the smaller number of molting males is insufficient to demonstrate the bimodal pattern observed in the more abundant females. Among both males and females, 65% of all molts occur during N and F lunar phases associated with "neap" tides in the Gulf of California. Further observations in the field are required to verify whether or not oviposition is correlated with lunar or tidal cycles. The divided lunar method of analysis produces only slightly less extreme patterns in the temporal distribution of molts and eggs in *G. sacae*.

G. falcatus (Hawaii)

In *G. falcatus* from Hawaii (Table I) no lunar or tidal molting synchrony can be demonstrated statistically, although there is a trend for both males and

females to molt during "spring" (57%) rather than "neap" (43%) tidal cycles. The distribution of molts across tidal cycles differs significantly from that in *G. zaccac* ($\chi^2 = 15.44^{**}$, $df = 1$) and *H. glyptocercus* ($\chi^2 = 5.49^*$, $df = 1$), but not from *P. ciliata* ($\chi^2 = 3.19$, $df = 1$), substantiating the tendency for *G. falcatus* to molt during "spring" tides.

Significantly more female *G. falcatus* lay eggs during "neap" than "spring" tides. Egg deposition occurs in significantly different tidal phases from molts in females ($\chi^2 = 5.62^*$, $df = 1$) and from molts in the population ($\chi^2 = 6.34^*$, $df = 1$).

Again, these data span different seasons of different years. Reproduction occurs year round in *G. falcatus* (personal observation; Kinzie, 1968). The failure to demonstrate significant synchrony of molting does not appear to be due to fading of the pattern, either at particular times of the year or after laboratory maintenance. All data also were analyzed using the divided lunar method, but no significant change in clustering of events in time was observed.

Haptosquilla glyptocercus (*Enicetok*)

H. glyptocercus demonstrates a strong tendency to molt during "neap" tides (Table I), although the data fall barely below the 0.05 level of significance. The distribution of molting in tidal cycles does not differ from that in *G. zaccac* ($\chi^2 = 0.72$, $df = 1$) but diverges from the tidal molting patterns observed in *G. falcatus* ($\chi^2 = 5.49^*$, $df = 1$) and *P. ciliata* ($\chi^2 = 9.77^{**}$, $df = 1$).

Pseudosquilla ciliata (*Hawaii, Florida, Thailand*)

P. ciliata, a circumtropical gonodactylid which is sympatric with *G. falcatus* in Hawaii, molts significantly more often during "spring" than "neap" tidal cycles (Table I). Populations of *P. ciliata* from Hawaii and Florida show similar patterns of molt timing ($\chi^2 = 1.50$, $df = 3$); most molts occur during the last phase of the moon. Eggs are laid during "neap" tides. A yearly and seasonal breakdown of these data, as well as lunar phases at collection, shows no relationship between collection and molting patterns.

During maintenance of *P. ciliata* in Thailand 2, 1, 1, 5 individuals molted in the N, I, F, L lunar periods, respectively (initial lunar method; note that Table III presents only field data). This pattern is not significantly different from that of *P. ciliata* from Hawaii and Florida ($\chi^2 = 0.45$, $df = 3$). However, in Thailand seven batches of eggs were laid in the laboratory during L (neap-spring transition during June-August), and one batch was deposited in F.

Species from Australia

Table II shows molting and reproduction in five sympatric species of Australian gonodactylids. The distribution of molting during spring and neap tidal periods does not differ among the five species ($\chi^2 = 4.71$, $df = 4$), although the sibling species *G. graphurus* and *G. falcatus* probably show different molting patterns ($\chi^2 = 3.65$, $df = 1$; $P = 0.04$, Fisher exact probability test). No lunar or tidal molting synchrony of the stomatopod community is demonstrated. Molting sample sizes are small, and the transfer during maintenance from the southern to the northern hemisphere could obscure a molting pattern if present. Molting was also

TABLE II
Molting and reproduction in five species of Gonodactylus from Australia. Analysis is by initial lunar and actual tidal cycle methods.

	Molts										Eggs					
	Initial lunar					Actual tidal					Initial lunar			Actual tidal		
	N	I	F	L	X ²	SPR	NP	X ²	N	I	F	L	X ²	SPR	NP	X ²
<i>G. graphurus</i>	7	7	6	2	3.09	7	15	3.10	0	4	0	4	—	7	1	—
<i>G. falcatus</i>	4	2	4	4	—	9	5	1.14	1	1	1	1	—	2	3	—
<i>G. smithii</i>	1	1	0	2	—	2	2	—	1	0	1	0	—	2	0	—
<i>G. hendersoni</i>	3	0	1	0	—	1	3	—	0	0	0	1	—	1	0	—
<i>G. affinis</i>	2	2	0	3	—	4	3	—	0	2	1	0	—	3	0	—
Total	17	12	11	11	1.94	23	28	0.49	2	8	3	6	4.78	15	4	6.36*

analyzed using the divided lunar method, and no change in clumping of events was observed. *G. graphurus* molts and lays eggs in opposite tidal cycles ($P = 0.009$, Fisher exact probability). Although untestable, time of egg deposition does not appear to vary among species. Oviposition across tidal phases is not significantly different in *G. graphurus* and *G. falcatus* from Australia ($P = 0.11$, Fisher exact probability). Analysis of egg deposition by all species across all four lunar categories, using both initial and divided lunar methods, fails to achieve statistical significance. Using the initial lunar method, $IL > NF$ ($\chi^2 = 5.56^*$, $df = 1$), indicating a probable correlation of egg laying with spring tides or the transition from neap to spring tides (see Fig. 1). Using actual tidal data, eggs of the five species occur significantly more frequently during spring than neap tidal cycles (Table II). All eggs except for one batch from *G. graphurus* were deposited in the field and laboratory in Australia soon after collection rather than after transport to North America.

Species from Thailand

Seven species of sympatric gonodactylids were collected and maintained in Phuket, Thailand. In contrast to the conditions for all of the above species, the period of maintenance was short. Large numbers of animals were differentially collected, maintained, and sacrificed during lunar cycles of these periods; therefore, the numbers alive during each lunar period were not necessarily comparable. To avoid this bias, Table III includes only field data. The number of individuals collected during each lunar or tidal phase provide the proportion of the molts and egg batches expected to occur in field collections during that phase for each species. In 1973, 77.8% of all individuals ($N = 447$) of all species were collected during new and full phases of the moon, but 100% of all molts ($N = 8$) found in the field occurred during new and full phases of the moon (initial lunar method). Molting showed similar patterns in 1973 and 1974. Table IIIA compares observed and expected frequencies of molting (1973 and 1974) during the transition from spring to neap tides (NF) and from neap to spring tides (IL), using the initial lunar method of analysis (Fig. 1). Data were analyzed also using divided lunar and actual tidal methods.

Field data alone demonstrate synchronization of molting with waning spring tides in *G. chiragra* (the only species for which sufficient numbers of molts allow testing). Analysis by the actual tidal method also shows significant correlation of molting in *G. chiragra* with spring tides ($\chi^2 = 10.72^{**}$, $df = 1$).

Also, significantly more individuals than expected in the Thailand stomatopod community molt during the transition from spring to neap tides (NF, initial lunar) and during spring tides (actual tidal method, $\chi^2 = 7.76^{**}$, $df = 1$). Although untestable, no significant differences in molt timing are apparent among species of the community, except perhaps *H. glyptocercus* and *P. ciliata*. Even if these two species do not follow the tendency for the rest of the community to molt during the transition from spring to neap tides or during spring tides, their influence is to bias the sample toward the null hypothesis rather than the alternate hypothesis.

If molts which occur within one to two weeks of capture are included in these field data, significantly more molts than expected still occur during spring than

TABLE III

Molting and reproduction in seven species of *Gonodactylidae* from Thailand. Analysis is by the initial lunar method for molting, and by the divided lunar method for oviposition. Only molts and eggs found in the field are included. The number of individuals collected during each tidal phase predicts the number of molts and eggs expected during that phase.

A. Molts observed and expected in the field (1973 + 1974).

	Number Collected		NF		IL		X ²
	NF	IL	Observed	Expected	Observed	Expected	
<i>G. viridis</i>	232	181	6	(3.9)	1	(3.1)	—
<i>G. chiragra</i>	143	199	18	(9.6)	5	(13.4)	12.61**
<i>G. smithii</i>	99	7	1	(0.9)	0	(0.1)	—
<i>G. falcatus</i>	101	11	3	(2.7)	0	(0.3)	—
<i>G. ternatensis</i>	34	25	5	(4.6)	3	(3.4)	—
<i>H. glyptocercus</i>	56	37	0	(1.2)	2	(0.8)	—
<i>P. ciliata</i>	66	21	0	(0.8)	1	(0.2)	—
Total	731	481	33	(23.7)	12	(21.3)	7.71**

B. Fresh egg batches observed and expected in the field.

(1973)							
<i>G. viridis</i>	161	30	10	(8.4)	0	(1.6)	—
<i>G. chiragra</i>	75	38	1	(0.7)	1	(0.3)	—
<i>G. smithii</i>	44	1	9	(8.8)	0	(0.2)	—
<i>G. falcatus</i>	44	10	5	(4.1)	0	(0.9)	—
<i>H. glyptocercus</i>	25	19	1	(0.6)	0	(0.4)	—
Total	349	98	26	(21.1)	1	(5.9)	5.29**
(1974)							
<i>G. viridis</i>	208	14	16	(15.9)	1	(0.1)	—
<i>G. chiragra</i>	159	70	0	(2.1)	3	(0.9)	—
<i>G. smithii</i>	57	4	2	(1.9)	0	(0.1)	—
<i>G. falcatus</i>	46	12	4	(3.2)	0	(0.8)	—
<i>G. ternatensis</i>	44	15	8	(6.0)	0	(2.0)	—
<i>H. glyptocercus</i>	42	7	7	(6.0)	0	(1.0)	—
<i>P. ciliata</i>	65	7	1	(0.9)	0	(0.1)	—
Total	621	129	38	(36.0)	4	(5.0)	0.31

neap tides in the community (actual tidal method, $\chi^2 = 4.78^*$, $df = 1$; $N = 57$ molts). However, laboratory maintenance increases scatter across lunar and tidal phases. Therefore, the effect of laboratory maintenance in general (such as for *G. zaca*, *G. falcatus*, *P. ciliata*, and the Australian community) should have been conservative, favoring the null hypothesis of no molting synchrony.

Although 78.0% of the individuals were collected during NF (divided lunar method) in 1973, 96.3% of all egg batches found in the field occurred during new and full lunar phases associated with spring tides (see Fig. 1, Table III). Also, if laboratory data (with expected values calculated from the number of individuals of each species alive in the laboratory during a given lunar phase) are included, more egg batches than expected were laid during spring than neap tidal phases in

1973 ($\chi^2 = 22.78^{**}$, $df = 1$; $N = 33$ batches of eggs). Use of the initial lunar and actual tidal methods show similar but less extreme trends for both field and laboratory egg data. Similar analyses in 1974, however, fail to show significant lunar synchrony of oviposition (Table IIIB). The heavy collecting bias in favor of spring tides relative to the small number of egg batches may account for this discrepancy, but conclusions await further verification.

The validity of the hypothesis of molting and reproductive synchrony in all of the above populations may be refuted by demonstrating bias in collecting and maintenance. Because of isolated maintenance conditions, social facilitation or chemical communication did not contribute to the results recorded in this study. There is no relationship between date of collection and pattern of molting during laboratory maintenance in any of the populations. Groups were collected during a single lunar phase, and it is difficult to see how this could impose a bimodal pattern of molting in the laboratory. Within species, groups collected in different lunar phases show similar molting patterns. Also specimens of *G. zaccac*, *G. falcatus*, and *P. ciliata* were maintained in the laboratory under the same conditions at the same time. While *G. zaccac* shows a strong bimodal molting pattern associated with neap tides, *G. falcatus* and *P. ciliata* exhibit a significantly different molting periodicity, indicating that laboratory regimes do not impose the observed molting pattern. In addition, field data from Thailand demonstrate tidal molting synchrony in *G. chiragra* and in the stomatopod community as a whole, excluding the effect of maintenance conditions. In fact, inclusion of molting data from the laboratory increases variation in the temporal pattern of molting. Hence, data analyzed from laboratory maintenance probably represent a conservative estimate of molting synchrony in the population.

The molting pattern does not seem to be biased by tidal reproductive rhythms, since oviposition does not appear to be correlated with a physiological stage of the molt cycle, and in *G. zaccac* the molting rhythm does not differ in reproductive and nonreproductive seasons. Different species show no consistent relationship between the lunar-tidal phase of molting and reproduction: *G. zaccac* molts and probably reproduces during "neap" tides. During maintenance in Thailand *P. ciliata* appears to both molt and oviposit during neap-spring transitional tides or last lunar phases. *P. ciliata* from Hawaii and Florida molts during "spring" tides (or the last lunar phase) but lays eggs during "neap" tidal cycles, and *G. falcatus* shows the same tendencies. *G. graphurus* molts during neap but oviposits in spring tidal cycles. In addition, molting and egg laying probably occur too infrequently to be intimately related, although they may be independently mediated by similar environmental cues. Molts occur about every three months to once annually in *G. zaccac* and *G. falcatus*, and may occur only every two years or more in smaller species. This author has never observed any female stomatopod to lay more than one batch of eggs in a year in the laboratory, although about 100 individuals of *G. zaccac* and *G. falcatus* were maintained in the laboratory for a year or longer. Agonistic behavior and coloration of the ovaries indicate that field populations of gonodactylids always have a high percentage of nonreproductive females even at the peak of the long or continuous reproductive season; the percentages of females with egg batches found in the field suggest that females of most species reproduce about once per year or less (Reaka, 1975c), although the population may repro-

duce in biannual peaks (Kinzie, 1968). Therefore, reproduction cannot be shown to structure tidal molting patterns.

In spite of the above arguments, the molting data derived from extensive periods in the laboratory may not be independent in some way which would make statistical testing based upon subsequent lunar or tidal groupings untenable (J. T. Enright, Scripps Institute of Oceanography, personal communication). There are several arguments against this objection to the data. First, I can identify no cause for lack of independence among molts which occur in the laboratory. Second, if a spurious correlation of molting data with a tidal cycle results from the influence of pooling data or from some unidentified extraneous factor, then one might expect this lack of independence to affect the grouped results in one species by chance, but it should not recur among the several different species which were maintained at different times and different years in the laboratory (Table I). Third, and most important, the results of molting in the laboratory are consistent with field data (Table III), and with tidal synchrony of reproduction. Oviposition series usually occurred within a relatively short period and therefore were not subject to factors acting over longer intervals which might introduce dependence among events and artificial grouping. Also, the laboratory data are intended to provide more complete information on the general problem of molting and reproductive synchrony in stomatopod populations, and not to argue that endogenous molting and reproductive rhythms persist precisely in phase with the moon for extensive periods in constant conditions. Detailed records of molting and reproduction are available in Reaka (1975c) or upon request from the author.

In conclusion, one is left to reject the null hypothesis of no molting synchrony until further verification.

DISCUSSION

A great body of literature supports the existence of biological clocks which govern a variety of cyclic functions in protists, plants and animals. Evidence supports both endogenous and exogenous control of these rhythms (*e.g.*, Brown, Hastings, and Palmer, 1970; Enright, 1970; Brown, 1972; Palmer, 1973, 1974). Most studies of tidal rhythms have concentrated on daily lunar or tidal cycles ("circalunadian" rhythms; Palmer, 1973). The significance of studies of circalunadian rhythms to the semi-lunar and tidal rhythms of molting and reproduction in stomatopods is first, that circalunadian rhythms, like circadian rhythms, have been shown to persist for remarkably long spans of time relative to their period length in controlled conditions, indicating either a strong endogenous component, an enduring entrainment effect from lunar or tidal conditions prior to or at collection, or a continuing environmental stimulus transcending "constant conditions" (see Reaka, 1975c, for a detailed discussion of this literature). Therefore, it seems reasonable to hypothesize that lunar or tidal rhythms occur in stomatopods, and that the length of time these rhythms persist (even weakly) in the laboratory, relative to the phase length of the environmental periodicity, is not unusual compared to the circalunadian rhythms exhibited by many marine species.

Secondly, the extensive literature on circalunadian rhythms provides information about proximate environmental factors which may act upon lunar and tidal rhythms (see Reaka, 1975c, for discussion). Imundation and exposure have little

effect in general upon entrainment of circalunadian rhythms; it seems unlikely that exposure during collection induced artificial molting and reproductive rhythms. Photoperiod and maintenance temperature in general have little effect upon circalunadian rhythms. Extreme temperature pulses or regular temperature cycles are known to induce circalunadian rhythms, but did not occur during collection and maintenance of mantis shrimp. Pressure changes and mechanical agitation may entrain circalunadian rhythms, are associated with changing tides, and could occur in the natural environment prior to collection of the species in this study; however, these should not have introduced artifacts during maintenance in the laboratory. It seems probable that local tidal conditions, perhaps in conjunction with innate cyclic processes (and pervading lunar effects cannot be ruled out), entrain molting and egg laying in the shallow reef habitat and that these physiological processes persist in the laboratory unaffected by collection.

The factors controlling longer term rhythms, such as semi-lunar, lunar, tidal, seasonal, or annual cycles, are more difficult to identify than those for daily rhythms. Tidal rhythms offer several difficulties since tides may be unpredictable, either daily or monthly, due to local topographical features as well as geographical area. Storms are common in tropical seas and have major effects upon local tides as well as upon photoperiods resulting from moonlight (see Barnwell, 1976, for discussion of the complexities of tidal form and implications for concepts of rhythms.) There is probably a selective advantage for a marine animal to possess a rather strong endogenous component, at least persistent entrainment to long term lunar or tidal cyclic phenomena. A scattered literature on long term lunar and tidal rhythms of activity, reproduction, and molting provides important information for evaluating the proximate factors which may affect rhythms in stomatopods and the ultimate factors which may operate in selection for reproductive and molting rhythms.

A sand beach isopod, *Exocirolana chiltoni*, shows persistent daily and monthly activity rhythms which are probably entrained by tidal height and mechanical agitation in association with an endogenous rhythm; light probably does not control these rhythms (Enright, 1972). A shrimp, *Anchistoides antiguensis*, swarms at the surface on nights following the new moon (Wheeler, 1937).

The correlation of reproduction with lunar cycles in marine species has been noted in a number of reviews (Korringa, 1947, 1957; Enright, 1970; Giese and Pearse, 1974). The European oyster releases larvae semi-monthly (Korringa, 1947, 1957). Synchronous courting and mating around the new and full moon in fiddler crabs (*Uca annulipes*, *U. triangularis*) allows the release of planktonic larvae on spring tides (von Hagen, 1970). A tropical, tree-dwelling grapsid crab (*Aratus pisoni*) and a land crab (*Cardisoma guanhumi*) release larvae during new and full moon periods (Warner, 1967; Gifford, 1962). The grunion (*Leuresthes tenuis*) spawns on sand beaches in California one to three hours after high tide a few days after each new moon from February to September (Walker, 1952). Protected from predation, the larvae develop in wet sand until they emerge during the next spring tidal cycle. At least two other species of fish (*Hubbsiella sardina*, *Galaxia attenuatus*) show lunar spawning (Walker, 1952).

Reproductive Pacific and Atlantic palolo worms of several genera swarm during specific lunar cycles of several months a year. Swarming in the Atlantic palolo,

Palola (*Leodice*) *fucata*, occurs a few hours after sunset of the first or more commonly the last quarter of the moon (Clark and Hess, 1940). *Platynereis dumerilii*, a polychaete from the Mediterranean, normally spawns during the new moon (Hauenschild, 1960). These studies suggest that maturity of the worm, water turbulence, and changes in photoperiod associated with moonlight control the lunar synchrony of spawning which results in synchronous development and subsequent reproduction. These rhythms have strong endogenous components and continue for a number of months in the absence of external cues, particularly if imprinting of the rhythm occurs early in the life of the individual.

Monthly or semi-monthly reproductive rhythms occur in some species of echinoderms but appear to be absent in other species. Populations of a sea urchin, *Diadema setosum*, from different areas of the Indo-Pacific show either monthly spawning in different lunar phases (Fox, 1923; Yoshida, 1952; Pearse, 1968, 1975), no detectable reproductive synchrony (Stephenson, 1934; Mortensen, 1937; Pearse, 1969), or semi-monthly spawning (Kobayashi and Nakamura, 1967). Populations of another diademid urchin, *Centrostephanus coronatus*, from the east Pacific reproduce in monthly reproductive synchrony, but spawn in different lunar phases in different years (Pearse, 1972, 1975), or in the same lunar but different tidal phases from year to year (Kennedy and Pearse, 1975).

An intertidal midge, *Clunio marinus*, pupates three to five days before maximum spring tides, emerges, mates and oviposits within a few hours of the extreme low tide during each new and full moon (Neumann, 1966, 1969). This genetically based reproductive rhythm is synchronized by tides in some populations and by photoperiod in others, and persists for several lunar cycles in constant conditions.

Several stages of the life cycle of a salt marsh pulmonate snail (*Melampus bidentatus*) are synchronized with spring high tides (Russell-Hunter, Apley, and Hunter, 1970, 1972). Individuals brought into the laboratory in the spring (lacking tidal submergence for ten semi-lunar cycles) aggregate, copulate, and lay eggs during the summer according to fortnightly cycles associated with the new and full moon. In the field larvae hatch in semi-lunar synchrony; hatching can be induced by several inundations. The larvae settle into the high intertidal habitat occupied by the adults two weeks later on high spring tides.

Exocirolana chiltoni occurs in a narrow zone of sand on the high intertidal beach (Klapow, 1972). In addition to daily and fortnightly activity patterns, field studies of this isopod demonstrate semi-lunar rhythms of feeding, parasitic infection, mating, release of young, and molting. Feeding and parasitism cycles result from rather than cause the molting rhythm. Synchronous breeding results in synchronous release of young and synchronous molting of the first stage manca two weeks later. The reproductive periodicity apparently subserves the primary adaptation of molting synchrony. Molting in the developmental stages occurs in phase with the molting periodicity of the adult population, and molting synchrony does not diminish among older individuals, even those which are more than one year old. The molting peak occurs in the week prior to new and full moons on rising spring tides in field populations, and persists less distinctly through at least one molt cycle in the laboratory. During rising spring tides, molting isopods are exposed briefly to desiccation and predation; however, on maximum or receding spring tides molting individuals, stranded high on the beach and lacking the ability to burrow into the sand, probably are killed.

A rocky intertidal isopod, *Lygia oceanica*, molts during neap tidal phases (Glaçon, 1968). The rhythm persists in the laboratory for at least eight tidal cycles. I divided the data presented by Glaçon into seven-day periods which encompassed the spring or neap tides. In successive spring and neap tidal cycles 6, 59, 22, 56, 19, 44, 24, 45 molts occur, respectively ($\chi^2 = 75.12^{**}$, $df = 7$; and $\chi^2 = 64.32^{**}$, $df = 1$, for spring and neap categories). These data represent comparable percentages of molts (26% spring, 74% neap) to those observed in the tidal phases in this study. The rocky crevices inhabited by *L. oceanica* are submerged only a few days each month, when these semi-terrestrial isopods emigrate to higher terrain to escape wave action and prolonged submersion. Individuals which molt during the spring tidal phase probably perish.

Some evidence suggests that a molting rhythm occurs in a shrimp (*Anchistoides*) which swarms and mates on nights following the new moon (Wheeler, 1937; Klapow, 1972). Nouvel (1945) finds increased numbers of molts immediately after spring tides and during the approach of the first and last lunar phases in a shrimp (*Leander serratus*) maintained in the laboratory. The prevalence of reproductive periodicities, and the frequent obligate relationship between breeding and molting in crustaceans, suggests that molting rhythms may be more common than usually thought.

These studies provide several conclusions of significance for the present analysis of molting and reproduction in stomatopods. First, long term lunar and tidal rhythms in marine organisms persist in the laboratory in the absence of environmental cues and appear to have strong endogenous components. Secondly, long term rhythms of activity, reproduction and development, and molting sometimes are entrained by long photoperiods resulting from the full moon, by inundation from high tides, and by turbulence. These rhythms frequently are entrained early in life, and subsequent cycles result from this early synchronization. Thirdly, the reproductive rhythm appears to maintain the primary molting rhythm in sand beach isopods. Although young crustaceans sometimes molt faster than older individuals, the entire population of sand beach isopods remains in molting synchrony. Similar phenomena appear to occur in stomatopods. Fourthly, as in the present study, reproductive synchrony in different populations may occur in different lunar phases (*e.g.*, urchins). In different years one population may spawn during different lunar phases, or during the same lunar but different tidal phases. Different populations (as in *Clunio*) may be either genetically or environmentally entrained to use different cues; or a complex interaction of lunar, tidal, or other factors may result in molting or spawning during different lunar phases. The important selective factor for many species may be synchronous spawning or molting among individuals by social or whatever cues are available for a given population.

The primary selective advantage for long term lunar or tidal rhythms of activity probably rests in feeding efficiency and increased mating opportunity. Synchronous reproduction correlated with lunar or tidal cycles may provide maximum mating efficiency and fertilization of gametes, particularly among sedentary, cryptic, nonabundant species, or species with external fertilization; and reproductive synchrony may allow simultaneous development and molting. Tidal reproductive synchrony may be associated with exploiting an area of the intertidal otherwise unavailable where young or adults encounter low competition or predation (*e.g.*,

grunion, midges). Availability of food for larvae and favorable currents for larval dispersal represent important but relatively unexamined factors which may govern tidal reproductive rhythms. Among intertidal organisms, physical factors such as temperature, dryness, and wave action may select for or against reproductive success of individuals which oviposit during spring or neap tidal cycles. Selection for synchronous molting in populations may be related to mating or may be imposed by physical damage, drowning, or desiccation when molts occur during inappropriate tidal cycles. Several hypotheses which may explain selection for molting and reproductive rhythms in stomatopods will now be examined.

If physical factors in intertidal or shallow water areas favor molting and reproductive rhythms, these rhythms should reflect the habitat and depth distributions of the respective species of stomatopods, and both molting and reproduction should occur during the same tidal cycle of least physical stress. Low intertidal regions suffer greatest exposure during spring tidal cycles but decreasing or no exposure during neap tidal cycles. Increasing height in the intertidal is accompanied by greater exposure during neap tidal cycles, whereas such areas are inundated once or twice daily during spring tides. Therefore, both molting and reproduction should occur during neap tides in species restricted to the low intertidal; in high intertidal species molting and reproduction should occur during spring tides.

Predation could impose selection for cyclicity in the shallow water environment, since time of exposure to fish predation is greatest during spring tides for high intertidal species, but greatest during neap tides for species occurring low in the intertidal. If displaced from their burrow, stomatopods would be most vulnerable to predators when incapacitated by brood care or especially by molting. Both molting and reproduction should occur in the opposite tidal cycle from the period of most intense predation. Therefore, species from low intertidal areas should molt and reproduce during spring tides, and species from high intertidal areas should molt and reproduce during neap tides.

Feeding cycles during tidal phases could impose selection for molting and reproductive rhythms. Feeding time for species which occur in the high intertidal area is restricted during spring tides, since individuals feed mostly on incoming and outgoing tides; during low water individuals remain in their burrows which are usually above the water line, and at high water fish predators abound in the area, making foraging dangerous. Feeding time for species in moderately high and in high intertidal areas is greatest during neap tides when shallow water excludes predators for a large percentage of the time. In low intertidal areas, feeding time is limited during spring tides by exposure at low water and by predators at high water, and throughout neap tides by predators. Stomatopods do not feed when molting or caring for eggs; molting and reproduction should be concentrated when feeding is disadvantageous or impossible. Species high in the intertidal should molt and reproduce during spring tides, and no synchrony is predicted for species from low intertidal areas.

Therefore, the *physical factors hypothesis* predicts molting and reproductive rhythms for high intertidal species during spring tides and for low intertidal species during neap tides; the *predation hypothesis* predicts rhythms for high intertidal species during neap tides and for low intertidal species during spring tides; and the *feeding time hypothesis* predicts rhythms for high intertidal species during

spring tides, but no rhythms for low intertidal species. The following analysis of stomatopod distributions indicates confirmation (+) or contradiction (-) of the predictions from each of these hypotheses, respectively. For example (+--) indicates that physical factors but not predation or feeding hypotheses explain the observed molting or reproductive rhythm in conjunction with the depth distribution of the species.

G. zacae occurs in coral rubble from low, occasionally exposed intertidal areas to at least 70 meters in depth; this species molts (+--) and probably reproduces (+--) during "neap" tides. *G. falcatus* occurs in moderately low intertidal coral rubble in Hawaii (exposed by moderate spring tides), in the low intertidal in Australia (exposed by low spring tides), and in the very low intertidal in the Marshall Islands, the Gulf of Thailand, and the Andaman Sea (where exposure occurs on very low spring tides). *G. falcatus* tends to molt during spring tides in Hawaii (-+-), Australia (-+-), and Thailand (-+-), and oviposits during "neap" tides in Hawaii (+--). *P. ciliata* occurs under and in coral rubble and vegetation over a fairly wide shallow subtidal and low intertidal habitat, but is most abundant in moderately high intertidal areas in Hawaii, Australia and Thailand. *P. ciliata* molts during "spring" tides (+-+), and oviposits (Hawaii and Florida) during "neap" tides (-+-). In Australia, five species of *Gonodactylus* occur in the low intertidal coral rubble which is exposed only during low spring tides. Although the other four species apparently are restricted to the low intertidal and shallow subtidal, *G. graphurus* occurs as deep as 30 meters. These species do not show molting rhythms (--+) but oviposit during spring tides (-+-). In Thailand, *G. ternatensis* is restricted to the extremely low intertidal coral and is rarely exposed. *G. falcatus* is exposed regularly, although briefly, by very low spring tides. *P. ciliata*, *G. smithii*, and *G. viridis* all co-occur with *G. falcatus* but extend into shallow intertidal areas as well. *H. glyptocercus* occurs from mid-intertidal coral rubble to high intertidal rock. *G. viridis* extends to high intertidal coral and rock, encountering extensive exposure during most low tides. *G. chiragra* extends upward from the moderately low intertidal rubble but predominates in the high intertidal rock, which is exposed for longer periods during neap than spring tides. *G. chiragra* molts significantly more frequently than expected during spring than neap tidal cycles in the field (+-+), as do all of the species of stomatopods in Thailand (-+-). Oviposition occurs during spring tides among these species (-+-).

Selection by physical factors correctly predicts the tidal cycle for molting or reproduction, given the species distribution, in five of thirteen cases; selection by predation explains seven of thirteen cases; and selection by feeding time explains three of thirteen cases. In the cases discussed above, molting and reproduction occur during the same tidal cycle in two of five cases. These data provide poor evidence that selection from physical factors, predation, or feeding time favors molting and reproductive synchrony.

The fourth explanation for the selective advantage of semi-lunar or tidal molting and reproductive synchrony, the *selfish herd hypothesis*, predicts that peaks of molting and reproduction may occur in either spring or neap tidal cycles in different populations from different geographical areas; that one population probably will show the same rhythmicity in high, low and subtidal areas, but will not necessarily molt and oviposit during the same tidal phase; and that different species

within a sympatric stomatopod community will show similar molting and reproductive rhythms. These predictions are mostly confirmed by the above data.

Hamilton's (1971) selfish herd hypothesis proposes that some social aggregations may result from avoidance of predators by individuals which hide among others of their own species. The present hypothesis for tidal molting synchrony is a temporal modification of the selfish herd hypothesis. Individuals which molt when most other individuals are also molting may suffer low mortality from aggressive congeneric and conspecific stomatopods.

Fighting and the hazards of molting are accentuated even early in ontogeny among stomatopods. Larval instars of *Squilla* attack, kill, and sometimes eat conspecifics, especially when the latter are molting (Alikumbi, 1950; Pyne, 1972). This aggressive behavior intensifies over ontogeny (Reaka, in preparation). If maintained communally, adult squillids and gonodactylids will kill and frequently devour a molting conspecific or congeneric. Individuals in the late premolt and early postmolt stages exhibit decreased dominance; recently molted individuals suffer extensive damage and frequent mortality during fights or handling. Displacement from a burrow by a conspecific or congeneric and exposure to predation may be even more dangerous than fighting injuries. Vulnerability at the molt is undoubtedly one of the selective pressures which favors plugging of the cavity entrance(s) and burrowing behavior as the molt approaches (Reaka, 1975a).

An advantage to the individual accrues if it is entrained genetically and/or environmentally to molt about the same time as the rest of the population. For an extreme example, consider that in a population of 100 animals, 99 molt within one lunar phase. Any individual that does not molt and remains out of phase with the population could invade, perhaps eat, and occupy the cavity of any of the 99 molting individuals in a species which does not seal the burrow or otherwise hide at molting. The probability that one of the molting individuals will be displaced or killed is only 1/99. However, when the asynchronous individual subsequently molts, the probability that it may be displaced or killed by the other 99 intermolt individuals is 99/100. A similar system would apply to the bimodal pattern established in *G. zaccac*, for example, but the margin of advantage would be smaller. If it is assumed that a constant number of individuals which molt are killed by aggression (*e.g.*, five during each of the four lunar phases), then it is obvious from Table I that an individual which molts during I or L would be selected against, since the probability of being killed would be 5/47, 5/19, 5/47, and 5/31 in the four lunar phases, respectively. In fact, the probability that an asynchronous individual will be killed is even higher because fewer individuals are molting during I and L, and therefore more voracious intermolt stomatopods are available to effect a greater number of killings during I and L (*e.g.*, 5/47, 8/19, 5/47, 8/31 or 11%, 42%, 11%, and 26% chance of mortality at the molt). Therefore, once initiated in the population, selection for molting synchrony should be a positive feedback spiral.

Because of low molting rates, a relatively small percentage of the population molts at a given time. However, natural selection should focus upon this segment of the population, favoring reception of cues which initiate molting at a time when most other individuals molt. Stomatopods (as well as lobsters and crabs) possess long mid- or subterminal stages of the molt cycle, followed by rapid completion of the stages preceding the molt (Reaka, 1975a). These observations suggest that

an individual may wait in subterminal stages of the molt cycle for a considerable time before rapidly completing the molt upon reception of appropriate stimuli. An individual may cheat, or pillage the surroundings during cycles of molting in the population, then molt in phase with the population. In fact, the population may be comprised of reciprocally cheating individuals. However, this only accentuates the advantage to an individual which responds opportunistically to cues, hides and/or seals its cavity, and molts when the maximum number of other individuals also are molting. This type of cheating is probably a natural consequence of intermolt intervals which span a number of peaks of molting in the population, and should not cause a collapse of the system of molting synchrony because each molting individual should still scramble to get to "the middle of the herd."

One effect of molt synchrony would be to provide a phasic sequence of predation by stomatopods and introduction of instability into the predator-prey environment. Johnson (1973) discusses phasic predation resulting from molt synchrony of damselfly naiads preying upon cladocerans. In stomatopods one would expect selection against molting synchrony if food limits the population; molting synchrony should introduce periods of increased and decreased competition for food among the predators. Population density of the stomatopods would be limited by the periods of high competition for food when few stomatopods are molting. Asynchronous molting would effect an average but stable level of competition for food, and density equilibrium of the stomatopods would be higher than above. Also, populations of the prey species would be maintained at low densities by the peak feeding phases in the intermolt cycle of a molt-synchronized predator. Populations of prey species might be extinguished by intense phasic predation, lowering prey diversity as well. Phasic molting and predation, even on a predictable basis, would probably break down in a population of stomatopods limited by food. Alternatively, if congeneric and conspecific competition for burrows (rather than food) limits populations of stomatopods, then molting synchrony is one of several possible adaptations which could decrease mortality associated with molting.

The initiation of molting synchrony in a population is more difficult to explain than the maintenance of this trait. Local populations, nondispersive larval behavior, and synchronous release and/or hatching of eggs could initiate molting synchrony. Several kinds of evidence suggest that these phenomena occur in gonodactylid stomatopods. *G. falcatus* and *G. zaca* are highly color polymorphic. Localized demes are uniform in body size and color relative to those on other patch reefs. Although *G. falcatus* was introduced to Oahu approximately 30 years ago, has increased markedly in density, and has displaced another gonodactylid (Kinzie, 1968), it has not colonized adjacent outer islands of the Hawaiian chain except for Molokai, in spite of available habitat on the other islands (personal observations; R. A. Kinzie, University of Hawaii, personal communication; W. VanHeukelem, University of Hawaii, personal communication). The behavior of larval stages of *Squilla* and *Lysiosquilla* keeps them near the substrate and in dark places (Alikunhi, 1950; Pyne, 1972). Gonodactylids possess fewer "pelagic" stages than squillids (Gohar and Al-Kholy, 1957). Although larvae of *G. bredini* reportedly become photopositive after the fourth instar (Dingle, 1969), other observations suggest that swimming activity is not sustained and therefore that larval dispersal may not be extensive (Pyne, 1972), particularly in the gonodactylids (personal observations). Therefore, molting synchrony could be established by

chance, and maintained by selection as discussed above, in small nondispersive populations. Also, oviposition rhythms may initiate molting rhythms. Synchronous hatching probably results from synchronous oviposition. Since synchronous hatching precedes synchronous molting and development in isopods, it is possible that the larvae of stomatopods develop synchronously without extensive dispersal, and therefore initiate local molt synchrony where they settle. Reproductive synchrony could evolve in response to other factors, such as availability of food for or predation upon larvae, or finding a receptive mate in a population where few individuals are reproductive at any one time. In addition, however, it seems likely that selection would favor those individuals which reproduce in a lunar or tidal phase and the young of which molt in phase with the population.

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SUMMARY

1. During laboratory maintenance, *G. sacae* from the Gulf of California molts during neap tides or the transition from spring to neap tides; oviposition probably occurs during neap tides or the transition from spring to neap tides. *G. falcatus* from Hawaii tends to molt during spring tides or the transition from neap to spring tides; oviposition occurs during neap tides or the transition from spring

to neap tides. Strong evidence suggests that *H. glyptocercus* from Eniwetok molts during neap tides or their approach. *P. ciliata* from three populations molt during the last lunar phase, providing the only substantive evidence for lunar rather than tidal control of molting in stomatopods. While *P. ciliata* from Hawaii and Florida lays eggs during neap or waxing neap tidal phases, those maintained in Thailand deposit eggs during waning neap tidal cycles. *G. falcatus* and *G. graphurus* from Australia molt in opposite tidal cycles; *G. graphurus* molts during neap tides but reproduces during spring tides. The five species of Gonodactylidae from Australia oviposit during spring tides.

2. Field data demonstrate significantly more molting during spring than neap tidal cycles in a gonodactylid community comprised of seven species in Phuket, Thailand. Laboratory maintenance increases variation in the pattern of molting across tidal cycles, although molting still occurs significantly more frequently in spring than neap tidal cycles. *G. chiragra* molts significantly more frequently than expected during spring than neap tides in the field. Both field and laboratory data demonstrate significant correlation of oviposition with spring tides among the species in 1973 but not 1974.

3. These data support a temporal selfish herd hypothesis that synchrony of molting in the population reduces mortality due to conspecific and congeneric aggression in stomatopods. Observed data do not support predictions from alternative hypotheses that physical factors, feeding, or predation impose molting and reproductive rhythms. Molting synchrony is more consistent with the idea that stomatopod populations are limited by the availability of burrows than by food. The initiation of molting synchrony in the population can be explained by selection for response to environmental cues, by chance, and/or by small, local populations with synchronous hatching of young. Oviposition rhythms therefore may subserve the primary molting rhythm.

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